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Sequential settlement and site dependence in a migratory raptor

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Habitat selection models, such as the ideal free, ideal despotic, site-dependent, and conspecific cuing models, are of great importance to behavioral ecologists given their capability to predict habitat distributions and to link individual behavior to population processes. However, there have been relatively few field tests of their predictions. We tested the 4 models by studying the process of sequential settlement on territory in 2 distant populations of a migratory raptor, the black kite *Milvus migrans*. Results were mainly consistent with the site-dependent model: on arrival, kites settled on progressively lower quality territories, and earlier arriving individuals were older, larger, and in better body condition than later arriving ones, leading to a state-dependent arrival sequence also predicted by a previous theoretical model of settlement pattern. Occupation of superior territories by superior phenotypes resulted in cascading advantages for earlier arriving individuals in terms of subsequent reproductive performance. At the population level, the populations expanded/retracted from lower quality sites during population increases/declines. The above scenario was consistent across the 2 populations, and a review of the literature uncovered a remarkably consistent picture of state-dependent arrival, progressive monopolization of best quality sites, and cascading effects on subsequent breeding performance. We propose as a general paradigm of sequential settlement the following process: 1) arrival date is a reliable surrogate of phenotype quality, 2) early-arriving individuals have preferential access to the best quality sites and partners, 3) the above conditions cascade into a number of benefits ultimately related to higher fitness for earlier arriving individuals. *Key words:* arrival date, dominance, ideal despotic, individual quality, *Milvus migrans*, preemption, site dependence, territory quality. *[Behav Ecol 18:811–821 (2007)]*

For territorial species, the acquisition of a good territory is an essential prerequisite for successful reproduction. Possession of a good territory may be conducive to higher mating success, a larger harem size, higher breeding success, higher probability of offspring recruitment, and higher fitness (e.g., Alatalo et al. 1984; Slagsvold 1986; Newton 1989; Hasselquist 1998; Currie et al. 2000; Forstmeier et al. 2001). Therefore, competition for territories will be frequently intense, and individuals will be selected to employ efficient tactics aimed at increasing their chances of access to high-quality territories so as to maximize their fitness.

In migratory species, the process of settlement on a breeding territory (hereafter "sequential settlement") is repeated every year, offering an ideal opportunity to investigate the causes and consequences of territory acquisition. In this context, some studies have highlighted consistent advantages of early arrival on the breeding grounds in terms of acquisition of high-quality sites (e.g., Aebischer et al. 1996; Petit LJ and Petit DR 1996; Hasselquist 1998; Kokko 1999). From a theoretical point of view, the process of sequential settlement has been traditionally framed into broader habitat selection models, namely the ideal free model and the ideal despotic model (Fretwell and Lucas 1970; review in Sutherland 1996; Newton 1998).

Under the ideal free model, fitness declines with density and individuals distribute themselves in a density-dependent manner so as to maximize their expected breeding success. On arrival from migration, the first individuals will occupy the best sites. As more individuals settle in, the growing density in the best patches depresses fitness expectations to the point that sites in a poorer habitat will be equally profitable and thus will start to be occupied. The final outcome is an equal average breeding reward across sites.

The ideal free model is probably unrealistic for territorial species in that individuals are assumed to move freely between patches. As a consequence, it has received little support in studies of breeding site selection (review in Newton 1998). The ideal despotic model was generated as a modification of the ideal free distribution to accommodate inequalities in competitive dominance among individuals (Fretwell 1972). Under this model, some individuals are capable, through aggression and territorial behavior, to relegate lower quality ones to poorer habitats. In this scenario, individuals arriving from migration will occupy territories according to their quality rank, resulting in a linear association between settlement order and territory quality. The model also predicts a significant variation in breeding performance across habitats because dominant individuals prevent local density from becoming so high as to depress their fitness. In a later variant, defined as the ideal preemptive model (Pulliam and Danielson 1991), individuals "monopolize" the best sites not by means of territorial behavior or overt aggression but simply by arriving earlier and preoccupying them.

More recently, the above models have been complemented with other ones based on conspecific cuing (Stamps 1988; review in Danchin et al. 2001) and site dependence (Rodenhouse et al. 1997, 2000). In the former, individuals settle on sites on the basis of the information provided by cuing on local conspecific density and productivity in the current and previous years. Site dependence was conceived as an extension of previous despotic and preemptive models (Fretwell 1972; Pulliam and Danielson 1991; Rodenhouse et al. 1997) but switched the focus from habitat patches to the more

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realistic, continuous variation in the quality of sites within such habitats. Under this model, individuals respond to heterogeneity in suitability by occupying sites adaptively and preemptively from best to worst in a linear sequence. Preemption implies no displacements, that is, once an individual occupies a site, it cannot be evicted. This simple mechanism, which does not necessitate direct interactions, generates negative density dependence as the population expands into or retracts from lower quality sites at respectively higher or lower density (McPeek et al. 2001).

The above 4 models mainly differ in the mode, scale, and targets of the selection process: ideal free and despotic models focus on mean performance of populations or subpopulations in coarse-scale habitat patches, site dependence focuses on individuals choosing small-scale sites, and conspecific cuing focuses on individuals selecting local clumps of neighbors. Furthermore, the models range beyond a simple description of settlement, by implying different forms of population regulation (e.g., Morris 1988, 1992; Rodenhouse et al. 1997; McPeek et al. 2001). For example, an increase in population density will be associated with a decline in mean site quality under the despotic and site-dependent scenario, with an increase in mean site quality under the conspecific cuing hypothesis, and with no directional change in site quality under the ideal free model (e.g., Morris 1994; Sutherland 1996; Stephens and Sutherland 1999). Despite such capability to integrate individual behavior and population processes and their obvious interest for ecologists, comprehensive field tests of the above models have been relatively few. For example, among the 57 studies on sequential settlement available to us, only 3 framed their analyses as tests of theoretical resource selection models (Lundberg et al. 1981; Petit LJ and Petit DR 1996; Pöysä 2001). Here, we provide such a test by examining the causes and reproductive consequences of sequential settlement in a migratory raptor, the black kite *Milvus migrans*. More specifically, we: 1) test whether arrival dates are related to territory quality and/or individual quality, 2) examine whether early arrival confers a subsequent reproductive advantage, and 3) assess the generality of our findings by conducting analyses on 2 distant populations from different biogeographic zones and by reviewing the studies on sequential settlement published so far.

Model species

The black kite is a medium-sized, opportunistic raptor. On return from migration, individuals settle on breeding territories, which usually include a nest site and an area of 50–200 m around it, whereas foraging occurs over wider, undefended (communal) areas (Cramp and Simmons 1980). In our study populations, territories differ substantially in quality and there is evidence that they are established on the basis of both direct assessment of quality and indirect assessment mediated by conspecific cuing (Forero et al. 1999, 2002; Sergio and Penteriani 2005).

METHODS

Study areas

Black kites' settlement dates were recorded between 1993 and 1999 in a 130-km^2 plot located along Lake Lugano (central Italian Alps) and between 1996 and 2000 in a 430-km^2 plot located in Doñana National Park (southwestern Spain). In the Lake Lugano plot, elevation ranged between 275 and 1125 m a.s.l., and the landscape was characterized by the open water of the lake and by mountain slopes covered by deciduous woodland, interspersed with cliffs and scarce open areas. In Doñana, elevation ranged between 0 and 32 m, and the landscape was characterized by seasonally flooded marshland, scrublands and grasslands, and mobile sand dunes along the seashore. Woodland was scarce and dominated by scattered cork oaks *Quercus suber* or stone pine *Pinus pinea* plantations. Climate was temperate continental in Lake Lugano (cumulative yearly rainfall between 1200 and 2100 mm) and Mediterranean subhumid in Doñana (250–1030 mm). Therefore, the 2 sites varied radically in elevation, landscape composition, seasonal dynamics, and climate. During the study period, populations at both sites were stable with a maximum number of simultaneously occupied territories of 44 in the Lugano plot and 531 in the Doñana plot.

Field procedures

In Lake Lugano, settlement date was recorded by observing all territories daily for at least 1 h from 10 March (when no territorial kite was ever present) to 15 April (no territory was ever occupied after 5 April). In 247 of 249 cases in which we checked a territory known to be occupied from a previous visit, the territory was confirmed as occupied within 20 min of observation. The 2 remaining cases were respectively confirmed within 1.5 h and within 30 min of observation the following day. Therefore, we consider any dating error to be negligible. This is because, on arrival, all birds were very conspicuous and displayed intensively, perched on traditional, dominant locations, and rapidly started nest building (Sergio and Newton 2003; see also Viñuela 1993). In all the 31 cases in which territories were occupied by individually recognizable birds (due to molting or broken feathers, unusual plumage, or other distinctive marks, e.g., missing claws), males occupied the territory before females (sexed by multiple observations of copulation behavior). Therefore, we assume that in this population the first partner to settle on territory was always the male.

The Doñana population is the subject of a long-term study on marked individuals (Forero et al. 1999, 2002). Since 1986, nestlings have been marked with a white plastic ring with a black, 3-character alphanumeric code, which can be read by telescope without disturbing the birds. By 2000, plastic rings had been placed on 4053 nestlings and 1054 adults captured with cannon nets (see below). Arrival date was estimated as the date of first observation of a territorial, banded individual. For the current analyses, we only retained data for intensively monitored territories that were regularly surveyed every 4–5 days ($n = 624$). Therefore, the dating error was larger than in the Lugano population but consistent across territories within the Doñana data set. Furthermore, in an ad hoc trial conducted in 2005 on a sample of 24 territories checked daily, the date of first ring reading of a banded individual was highly correlated with the date of territory occupation ($r = 0.88$, $P < 0.0001$). Individuals were sexed by molecular analysis of a blood sample (Sergio F, Blas J, Forero MG, Donazar JA, Hiraldo F, unpublished data) or by multiple observations of copulation behavior. To detect potential cases of later arriving birds expelling earlier settlers from a territory, the rings of marked territory holders were repeatedly read throughout the prelaying period. Hereafter, we refer to such contests as "takeovers," to the expelled bird as the "evicted" and to the new occupant as the "winner."

In both populations, nests were found by observing nest-building activities. Laying date was estimated by: 1) backdating nestlings from feather development when <6 days old in the Lake Lugano population (Sergio 2003) or 2) by a linear regression relating the length of the eighth primary to the age of the nestlings in Doñana (Viñuela and Bustamante 1992; Forero et al. 2002). Reproductive output was expressed as the number of young raised to fledging age (40–45 days old).

Individual quality

We used age, body size, and an index of body condition as estimates of individual quality (only available for the Doñana population). Age was available for a subsample of 468 individuals ringed as nestlings. Furthermore, many adults were captured on arrival using cannon nets as part of a long-term study on the species and under legal permit from the "Ministerio de Medio Ambiente—Dirección General para la Biodiversidad" (e.g., Forero et al. 1999, 2002). For the trapped adults, we used tarsus length as a measure of skeletal size (Garnett 1981; Alatalo et al. 1984; Hasselquist 1998). As body mass varied with year, breeding stage, and tarsus length, we standardized it by using the residuals of such relationships as an index of body condition (e.g., Schulte-Hostedde et al. 2005).

Habitat and territory quality

A potential problem in testing habitat selection models lies in finding a priori estimates of habitat and site quality. For example, estimating territory quality by its mean breeding success precludes the possibility to examine the effect of site quality on reproduction and confounds settlement decisions based on expected reproductive rewards (Petit LJ and Petit DR 1996; Rodenhouse et al. 1997; Pöysä 2001). We estimated territory quality as the first component (PC1) of a principal component analysis (PCA) (Tabachnick and Fidell 1996) conducted on 2 variables: the percentage of years that a territory was occupied (factor loading: $r = 0.72$ for Lake Lugano and 0.76 for Doñana) and the distance to the nearest wetland (factor loading: $r = -0.52$ for Lake Lugano and -0.62 for Doñana). The occupation rate of a territory has been recently shown to be a consistent measure of territory quality in a wide range of species, including black kites (review in Sergio and Newton 2003). Territory occupation rates refer to the period 1992–2003 for Lake Lugano (mean years of occupation ± standard error [SE] = 7.2 ± 0.5, range 1–12 years) and 1989–2000 for Doñana (4.9 ± 0.4, range 1–12 years). Proximity to wetland ranged between 70–7180 m in the Alps (mean ± SE = 2142 ± 143) and 1–360 m in Doñana (608 ± 28) and was chosen because 1) black kites have been repeatedly shown to be strongly associated with wetlands (Sergio et al. 2003, 2003a, 2003b; Sergio, Blas et al. 2005), b) their diet is usually dominated by wetland prey (Espina 1984; Hiraldo et al. 1990; Sergio et al. 2003b), and c) their foraging effort and performance peaks over wetlands (Hiraldo et al. 1990; Sergio et al. 2003a, unpublished telemetry data). Therefore, wetlands can be considered as optimal foraging habitat, and sites nearer to wetlands should afford superior access to optimal hunting grounds. Because nest predation rates in our populations may be intense (Sergio et al. 2003; Sergio, Blas et al. 2005), we added as a further estimate of site quality the number of predation events experienced at a territory in the previous 5 years (hereafter "predation risk"). This measure was not correlated with other estimates of site quality (all $r < 0.04$, $P > 0.05$) and thus was not included in the above PCA.

In ideal free and despotic models, individuals chose habitat types rather than the sites within them (Rodenhouse et al. 1997). To provide such a coarser measure, we assigned territories to 2 patch types: a wetland habitat and an inland habitat, including sites located within or beyond 1 km of the nearest wetland, respectively. The measure of 1 km was chosen because foraging during breeding is concentrated within 1 km of the nest (Sergio et al. 2003a; Sergio, Blas et al. 2005).

Statistical analyses

To pool data from different years, we assigned a value of 1 to the first day of observation of a territorial kite in each year and rescaled all later dates accordingly. To investigate any directional variation in phenotypic quality with arrival date, we related the latter to age, body size, and body condition by means of multiple regression (Tabachnick and Fidell 1996). We tested the effect of body size and condition separately from the effect of age because the formers were not related to the latter ($r < 0.23$, $P > 0.05$) and because this allowed to maximize the sample size available for the age effect (morphometrics were only available for a limited subsample of birds of known age and for which arrival date had been recorded). To test whether birds settled by direct evaluation of habitat type, territory quality, or by conspecific cuing, we used a multiple regression to relate arrival date to 1) habitat type (wetland vs. inland); (2) territory quality (PC1 and predation risk); and 3) variables related to conspecific cuing, including 3a) the distance to the nearest neighbor, 3b) the number of conspecific pairs within 200, 400, and 1000 m of the nest, and 3c) the mean number of fledged young in the previous year by all pairs within 200 and 400 m of the nest. The radii of 200, 400, and 1000 m were chosen because previous analyses have highlighted their importance for decisions related to territory establishment and conspecific cuing (Forero et al. 1999, 2002; Sergio et al. 2003, 2005; Sergio and Penteriani 2005). Because kites are site faithful (Forero et al. 1999, 2002) and previous residence may increase the attractiveness of a territory to its previous owner, we included in the above models previous residence as an additional dichotomous explanatory variable, so as to test and to control for the effect of site fidelity. Also, because territory quality may change among years (Lõhmus 2003), we added the categorical variable year and its interaction with territory quality as explanatory variables. To evaluate whether the effect of individual and territory quality were interactive, we fitted habitat type, territory quality, estimates of conspecific cuing, previous residence, age, year, and their interactions to a multiple regression with arrival date as the dependent variable. Finally, to examine the reproductive advantages of early arrival, we related the number of fledged young to settlement date, territory quality, estimates of conspecific cuing, age, prior residence, year, and their interactions.

To better discriminate between the despotic and preemptive mechanisms of territory acquisition, we compared the age and body measures of the evicted and winner individuals of territory takeovers observed during the settlement process. Most takeovers were detected because a marked bird displaced on arrival a nonmarked one or viceversa, which prevented a matched test between the 2 direct opponents. Therefore, we conducted a logistic regression with takeover outcome (winner or evicted) as the dependent variable and year, sex, prior residence, age, and their interactions as the explanatory variables. Body measures were available for too few individuals and were thus examined only by means of univariate comparisons. All the cases of takeovers were excluded from all the other models because of the uncertainty in assigning the settlement date of the evicted or of the winning individual to each territory.

To test whether each population expanded into or retracted from lower quality sites at higher density, we 1) calculated the average quality (mean values of PC1) of the sites occupied in year x and 2) related it to density in year x by means of univariate correlations. For this analysis, data were available for the period 1992–2004 for Lake Lugano and 1989–2000 for Doñana.

To check the generality of our findings we reviewed published studies on sequential settlement by 1) searching the Zoological Record and 2) looking for relevant papers cited in the initial batch of publications. Because many papers were detected in the latter way and because they frequently

targeted sequential settlement as part of a wider work focused on some other theme, we may have missed some relevant studies. Therefore, the review presented in Table 3 is assumed to be a random sample of the studies published so far on sequential settlement. For each paper, we asked the following questions and tested the preponderance of positive answers by means of a binomial test (Sokal and Rohlf 1981): 1) Is arrival date related to individual quality (measured as age, body size, or condition)? 2) Do earlier arriving individuals settle on the best territories? 3) Is early arrival associated with better breeding output? When variables included multiple measures (e.g., individual quality measured as age and also body size in different tests by the same authors), we used the nonsignificant measure in calculating the probability of the binomial test, so as to keep the test conservative. For example, in the study by Currie et al. (2000) listed in Table 3, the relationship between arrival date and individual quality was significant for age but not for body condition, and the study was classified as a "0" in applying the binomial test, implying a nonsignificant overall relationship between the 2 variables.

All multiple and logistic regressions were built through a generalized linear mixed models (GLMMs) procedure (Littel et al. 1996), which allows to incorporate independent variables as random effects in the model. In our case, as we sampled some individuals and territories repeatedly through the years, we fitted individual identity, territory identity, and year as random terms (the degree of pseudoreplication was anyway low, and parallel models built by using one randomly chosen observation per individual yielded the same conceptual results). All GLMMs were built through the Macro GLIMMIX of SAS (Littel et al. 1996). The GLMMs (with normal errors and an identity link function, poisson errors and a logarithmic link function, or logit errors and a binomial link function) were built by a backward elimination procedure: following Crawley (1993), all explanatory variables were fitted to the model, extracted one at a time from such a maximal model, and the associated change in model deviance was assessed by an *F*-test. In some cases, we built the same model in 2 or more alternative ways, for example, fitting the variable year as a random or as a fixed effect. In such cases, we compared models through an information-theoretic approach and selected the one with the lowest Akaike Information Criterion (Burnham and Anderson 1998). Throughout, we conducted separate models for males and females, because decisions related to territory establishment may differ between the sexes. For example, because in many bird species males arrive from migration before females, the former are likely to choose territories, whereas the latter may choose males, territories, or both (review in Morbey and Ydenberg 2001).

RESULTS

Settlement pattern

In Lake Lugano, the population built up very rapidly, reaching a plateau within less than 20 days (Figure 1a). Even if males always occupied territories before females (see Methods), the arrival dates of the 2 sexes largely overlapped (Figure 1a). In Doñana, the population built up rapidly at first, but new settlements spanned a period of about 2 months (Figure 1b). This was not an artifact of the methodology involved because 1) the appearance of newly established territories late in the season was confirmed by ad hoc data collected daily in 2005 and 2) the differential synchrony in arrival dates of the 2 populations mirrored their differential synchrony in laying dates (range of laying dates = 35 days in Lake lugano and 81 in Donana). In Doñana, male and female arrival dates did not differ significantly for 162 pairs for which arrival dates were collected for both of the marked partners (paired *t*-test: $t_{161} = 0.75$, $P = 0.45$; Figure 1b). Finally, in both populations, arrival dates of the 2 partners of a pair were positively intercorrelated (Lake Lugano: $B = 0.61 \pm 0.03$, $F_{1,90} = 311.90$, $P < 0.0001$; Doñana: $B = 0.46 \pm 0.06$, $F_{1,53} = 63.72$, $P < 0.0001$).

Arrival and individual quality

For both sexes, older individuals arrived earlier than younger ones (males: $B = -1.29 \pm 0.29$, $F_{1,108} = 19.97$, $P < 0.0001$; females: $B = -1.92 \pm 0.35$, $F_{1,106} = 30.57$, $P < 0.0001$; Figure 2). Furthermore, arrival date was related to body condition for males ($B = -17.43 \pm 4.80$, $F_{1,14} = 13.18$, $P < 0.05$; Figure 3a) and body size for females ($B = -0.07 \pm 0.03$, $F_{1,91} = 5.68$, $P < 0.05$; Figure 3b).

Arrival and territory quality

In both sexes and in both populations, territory quality was the only significant predictor of the date of settlement on territory (Table 1; Figure 1c,d). When we added to the explanatory variables of the above models age and its interaction with territory quality or with estimates of conspecific cuing, the models were unchanged for both sexes.

Territory takeovers

In all the 8 cases in which we directly witnessed a territory takeover, this was accompanied by physical fighting. In 3 cases, this escalated into talon locking, with individuals grasping each other's talons in flight and falling to the ground, where fighting continued until one of the contestants escaped. In 7 cases, an individual was evicted despite occupying that territory in the previous year. In univariate comparisons, the winners of takeovers were older and had a higher probability of previous residence on the contested territory than the evicted individuals (Table 2). Also, all the body measures of winners were larger than those of evicted birds, although none of these comparisons was significant (Table 2). Finally, age was the only variable to enter the stepwise logistic regression with contest outcome (evicted vs. winner) as the dependent variable ($B = 0.23 \pm 0.09$, $F_{1,19} = 5.52$, $P < 0.05$). The effect of previous residence thus disappeared when age was taken into account.

Reproductive consequences of early arrival

In both sexes and populations, laying date was positively related to arrival date (in all cases $B \geq 0.15 \pm 0.07$, $F_{1,17–36} \geq 5.65$, $P \leq 0.025$) and breeding output declined significantly with arrival date ($B \leq -0.03 \pm 0.001$, $F_{1,75–144} \geq 32.43$, $P \leq 0.0001$; Figure 1e,f). When we fitted arrival date, territory quality, and estimates of conspecific cuing to a multiple regression with breeding output as the dependent variable, territory quality was the only variable to enter the stepwise model for both sexes in the Lake Lugano population (Table 1). For the Doñana population, we added to the explanatory variables age and its interaction with arrival date, territory quality, estimates of conspecific cuing, and previous residence. For females, breeding output declined with arrival date (Table 1), whereas for males it declined with arrival date and increased with territory quality and age (Table 1). The interaction of age and territory quality was also significant: high breeding output could also be achieved by young males when these had access to high-quality territories or by older males when these happened to occupy low-quality territories.

Population-level effects

In both populations, the mean annual quality of occupied territories was negatively related to density (Lake

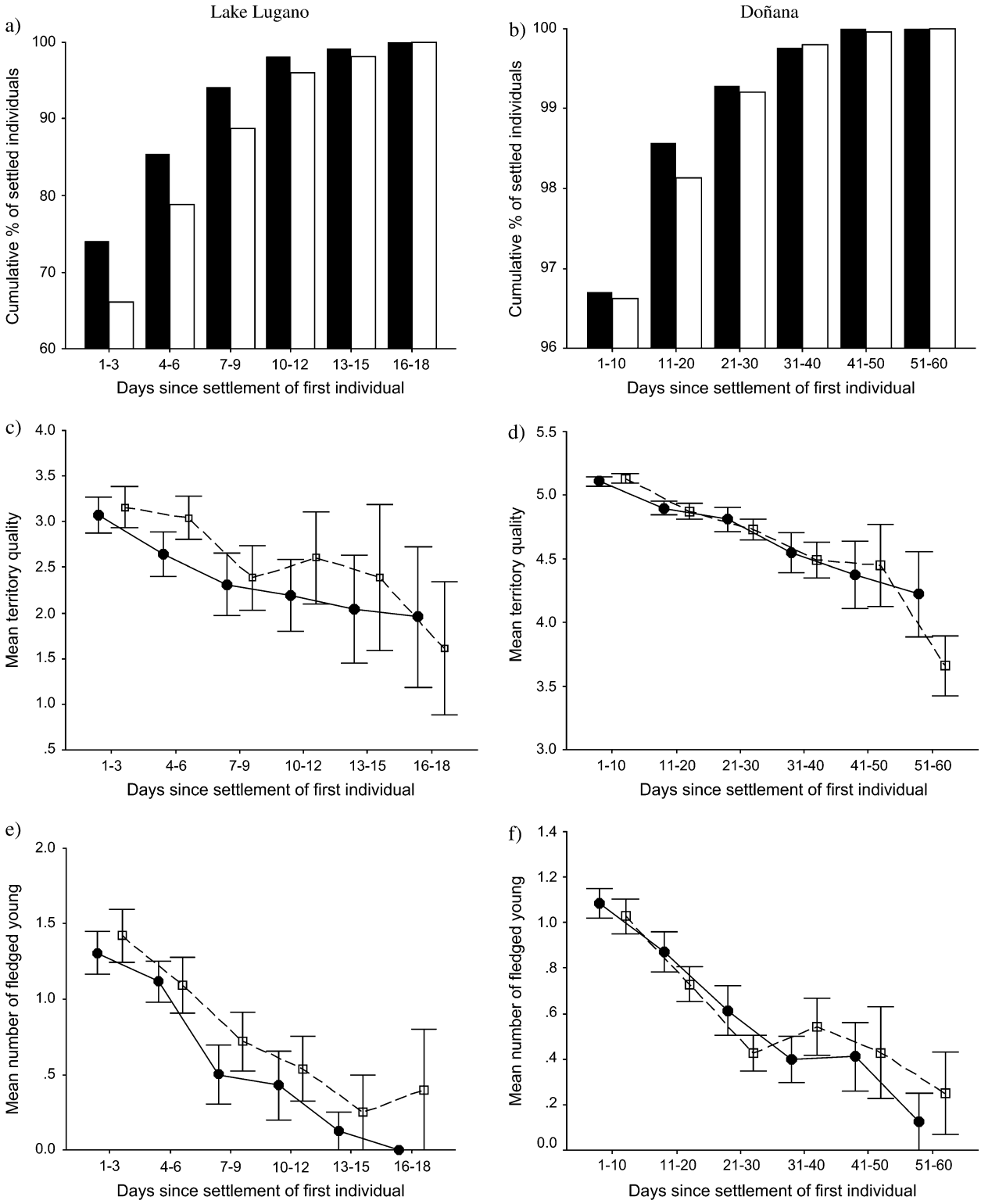

Figure 1
Settlement on territory in 2 black kite populations breeding in Lake Lugano (Italian Alps, 1993–1999, (a), (c), and (e) on the left) and in Doñana National Park (southwestern Spain, 1996–2000, (b), (d) and (f) on the right). In all graphs, filled symbols refer to males and open symbols to females. (a, b) Cumulative distribution of settling individuals. (c, d) Progressive decline in the mean quality of occupied territories along the settlement sequence (Lake Lugano: $n = 189$ males and 136 females; Doñana: $n = 365$ males and 359 females). Territory quality was estimated as the first component of a principal component analysis (see Methods) and rescaled in the figure so as to yield only positive values. (e, f) Progressive decline in mean breeding performance along the settlement sequence (Lake Lugano: $n = 189$ males and 136 females; Doñana: $n = 215$ males and 217 females). Bars represent 1 SE.

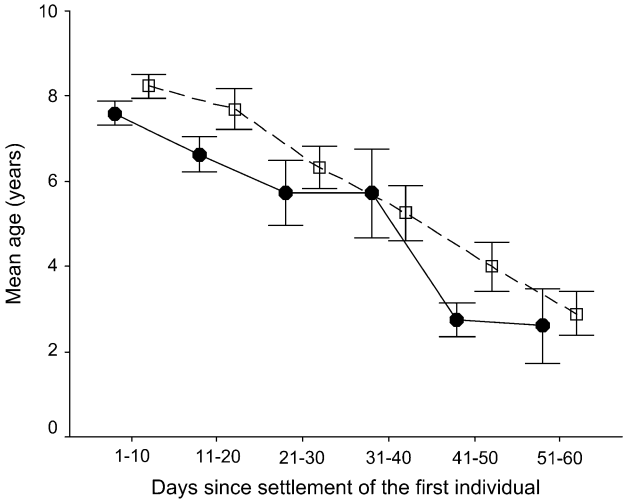

Figure 2
Progressive decline in mean age of territory holders along the sequence of sequential settlement in the black kite population of Doñana National Park (Spain). Filled cirlces = males ($n = 235$); open squares = females ($n = 233$). Bars represent 1 SE.

Lugano: $r = -0.64$, $n = 14$ years of study, $P = 0.01$; Doñana: $r = -0.65$, $n = 12$, $P = 0.02$).

Review of previous studies on sequential settlement

Data were available for 57 studies, 30 of which tested at least one of the relationships listed in Table 3. For all the examined variables, there was a strong consistency among studies in the obtained results (Table 3), with a significant preponderance of papers that reported a negative association between arrival date and 1) individual quality (reported by 82% of the studies that tested such relationship, binomial test, $P = 0.013$); 2) the quality of the territory occupied (92% of the studies; $P = 0.003$); and 3) breeding performance, independently of this being expressed as mating success (100%; $P = 0.002$), laying date (84%; $P = 0.004$), or number of offspring raised to independence (81%; $P = 0.021$, Table 3). Furthermore, the few cases that departed from the above trends often represented relatively unusual circumstances, such as years of extremely low-breeding success for the study population (Cristol 1995) or a study focusing only on the yearlings' subsector of the population (Schieck and Hannon 1992), which may or may not be representative of the processes at the whole-population level.

DISCUSSION

In both populations, there was a pronounced variation in quality values among territories. For example, site occupation rate varied between 8 and 100%, whereas the distance to the nearest wetland varied between 1 and 8360 m. Black kites recognized such gradients and settled accordingly, occupying progressively lower quality territories in a linear sequence (Figure 1c,d). Such process supported both the site-dependent assumption of adaptive settlement (Rodenhouse et al. 1997; McPeek et al. 2001) and the "ideal" assumption of theoretical habitat selection models, by which individuals are expected to have good knowledge of the variation and distribution of site quality (Fretwell and Lucas 1970; Kokko 1999; see also Zimmerman et al. 2003). As a result, early arrival implied access to a high-quality territory, as previously pointed out in other studies (Table 3), with consequent cascading effects on subsequent reproduction (see below). This raises the question of why did not later arriving individuals invest more in advancing their arrival date. The latter is the result of the timing and efficiency of migration and is probably promoted by 1) early accumulation of sufficient body reserves to depart from the wintering quarters, 2) rapid migration speed and optimal choices along the route, 3) social dominance at stopover sites, and 4) high-feeding efficiency to counter the costs of potentially unfavorable conditions during the migration journey (e.g., Berthold 1993, 1996). All the above characteristics are likely to be met by more experienced, older individuals of larger size and/or in better physical condition (e.g., Gwinner 1990; Lindström et al. 1990; Beletsky and Orians 1993; Fransson 1995; Marra 2000). As a result, only high-quality phenotypes will be able to meet the high risks and energetic demands of early arrival. Under this scenario, settlement date would function as a surrogate of individual quality, as predicted by theoretical models (Kokko 1999) and consistent with the findings of various empirical studies (e.g., Møller 1990; Rätti et al. 1993; Marra et al. 1998;

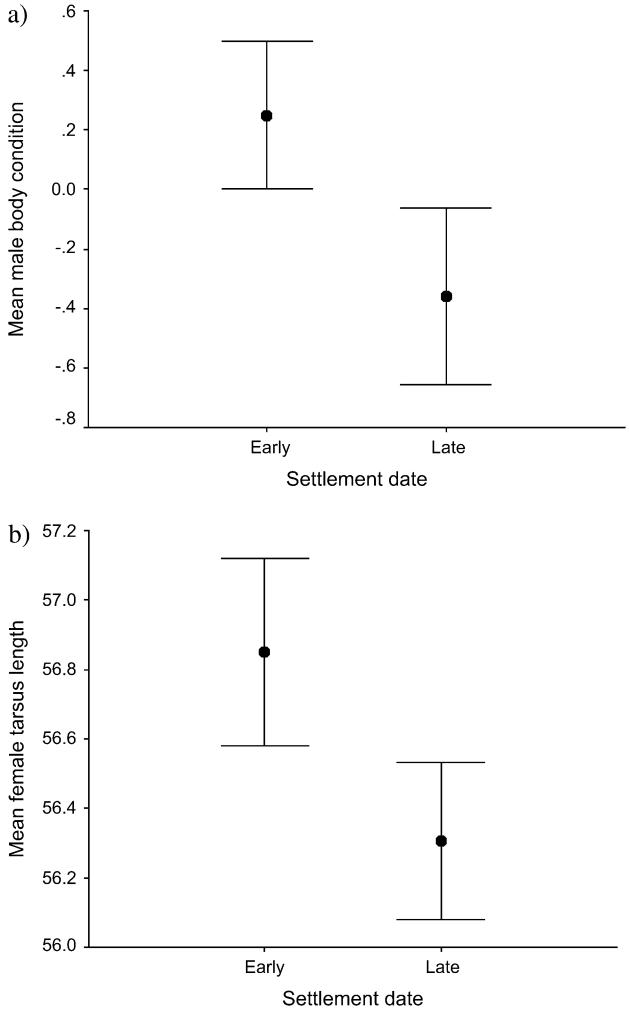

Figure 3
Mean body size and condition of male (a) and female (b) black kites in relation to their settlement date on territory in Doñana National Park (Spain; $n = 47$ males and 215 females). Individuals were classified as early or late settlers when they arrived from migration before or after the mean settlement date of the population. Body condition was estimated as the residuals of the regression of body mass on tarsus length, while controlling for year and breeding stage (see Methods). Bars represent 1 SE.

Table 1
Predictors of settlement date and breeding output of male and female black kites in 2 distant populations

Variable	Parameter estimate ± SE	*F*	*P*
Predictors of arrival date in Lake Lugano			
Dependent variable: male arrival date[a] ($n = 189$)[b]			
Territory quality (PC1)	–0.28 ± 0.05	31.45	<0.0001
Intercept	2.50 ± 0.14	—	—
Dependent variable: female arrival date[c] ($n = 136$)[b]			
Territory quality (PC1)	–2.13 ± 0.44	22.97	<0.0001
Intercept	11.61 ± 1.49	—	—
Predictors of arrival date in Doñana			
Dependent variable: male arrival date[a] ($n = 365$)[b]			
Territory quality (PC1)	–5.14 ± 0.70	53.85	<0.0001
Individual identity[d]	51.68 ± 15.91	3.25	<0.001
Intercept	47.96 ± 4.67	—	—
Dependent variable: female arrival date ($n = 359$)[b]			
Territory quality (PC1)	–7.68 ± 0.81	90.18	<0.0001
Individual identity[d]	47.69 ± 17.13	2.78	<0.01
Territory identity[d]	45.78 ± 17.34	2.64	<0.01
Intercept	54.08 ± 4.20	—	—
Effect on breeding output in Lake Lugano			
Dependent variable: male breeding output ($n = 189$)[e]			
Territory quality (PC1)	0.65 ± 0.11	35.87	<0.0001
Intercept	–2.15 ± 0.56	—	—
Dependent variable: female breeding output ($n = 136$)[e]			
Territory quality (PC1)	0.60 ± 0.12	23.75	<0.0001
Intercept	–1.72 ± 0.60	—	—
Effect on breeding output in Doñana			
Dependent variable: male breeding output ($n = 215$)[e]			
Territory quality (PC1)	51.68 ± 15.91	8.27	<0.005
Arrival date[a]	−0.02 ± 0.01	10.60	<0.005
Age	0.36 ± 0.16	4.86	<0.05
Interaction term: territory quality × age	–0.05 ± 0.03	4.32	<0.05
Intercept	3.82 ± 1.49	—	—
Dependent variable: female breeding output ($n = 217$)[e]			
Arrival date	−0.19 ± 0.05	16.26	<0.0001
Intercept	−1.67 ± 2.28	—	—

Random effects are only shown when their effect was significant.

[a] Variable $\log_e$ transformed.

[b] GLMM multiple regression with normal errors and a identity link function (Littel et al. 1996).

[c] Variable square root transformed.

[d] Random factor, effect tested by means of a *Z*-test (Littel et al. 1996).

[e] GLMM multiple regression with poisson errors and a logarithmic link function (Littel et al. 1996).

Currie et al. 2000; review in Table 3). Our results confirmed the phenotypic superiority of early-arriving birds, which were older, larger, and in better body condition than later ones, leading to a state-dependent sequence of settling individuals (Kokko 1999). Furthermore, the winners of physical contests over territories during settlement (takeovers) were older and possibly larger. This would decrease the potential advantage for a low-quality individual to invest in the advancement of its settlement date, given the high likelihood of subsequent eviction by an older bird. Such interactions may further guarantee the tight association between arrival date and individual quality.

Early occupation of good territories by superior phenotypes implied consistent advantages in terms of subsequent breeding output. Numerous previous studies have highlighted the benefits of early arrival in terms of 1) access to higher quality partners (e.g., Alatalo et al. 1984; Potti and Montalvo 1991; Currie et al. 2000; Forstmeier 2002), 2) earlier laying (review in Table 3), 3) higher breeding success (review in Table 3) and 4) higher levels of offspring recruitment (Hasselquist 1998; Currie et al. 2000). Furthermore, the fact that early-arriving individuals may be superior phenotypes and that such characteristics often have a genetic basis implies that the pairing with early-arriving individuals (in turn promoted by early arrival) will not only facilitate direct access to material resources (such as good territories with high food availability) but also yield indirect benefits in terms of production of "attractive" offspring (sexy son hypothesis, Weatherhead and Robertson 1979).

In conclusion, state-dependent arrival provided cascading advantages for early settlers, such as access to a better territory and mate, earlier laying, and higher offspring production. All the above is consistent with an early determination, within a breeding season, of the sector of the population with the best chances of successful reproduction. Therefore, for migratory species, the settlement period may act as an initial bottleneck selecting the subsector of individuals able to contribute offspring to future generations. In this sense, a phenotype investment in early arrival may reflect a short-term "career decision" with important repercussions on the longer, lifetime scale of its ontogenetic trajectory (Wiley 1981; Ens et al. 1995).

Toward a general pattern of sequential settlement

In both populations, there was support for a site-dependent pattern of settlement on territory. On arrival, individuals responded to heterogeneity in site quality by selecting territories adaptively from best to worst, breeding output varied in

Table 2

Age, body measures, and prior residence of black kites displaced from an occupied territory (evicted individual) by a later settler (winner individual)

Variable	Individual status		t	P
	Evicted (n)	Winner (n)		
Age (years)	5.21 ± 0.39 (34)	7.11 ± 0.60 (35)	−2.65	0.01
Tarsus length (mm)	55.14 ± 1.65 (14)	56.49 ± 0.89 (15)	−0.71	0.49
Mass (g)	870.4 ± 46.5 (14)	920.0 ± 40.8 (15)	−0.80	0.43
Body condition[a]	−10.4 ± 38.6 (14)	9.7 ± 37.9 (15)	−0.37	0.71
Prior residence[b]	17.5% (40)[b]	40.5% (37)[b]	5.00[c]	0.03

For conciseness and clarity of presentation, individuals of the 2 sexes are pooled in the table because they were equally represented in each sample (binomial test, $P > 0.05$) and because the effect of sex on the probability of winning a takeover was not significant ($\chi^2 = 0.003$, $P = 0.95$, see also Results). Means are given ± 1 SE.

[a] Residuals of body mass on tarsus length, breeding stage, and year (see Methods).

[b] Percentage of individuals that occupied the contested territory in the previous year.

[c] Difference tested by means of a χ^2-test on the count data.

parallel across sites, individuals changing territories from 1 year to the next moved to higher quality sites in an adaptive manner (Forero et al. 1999) and, when density increased or declined, the population expanded into or retracted from lower quality sites. Furthermore, individuals responded to the continuous variation in the suitability of small-scale sites rather than to the dichotomous variation in the mean quality of coarse-scale habitat patches typical of the "ideal" models (see Introduction). The advantage of such a site-dependent framework is that it focuses on the behavioral choices of individuals, which are the demographic units on which selection and regulatory processes operate (Rodenhouse et al. 1997, 2000; McPeek et al. 2001; Rodenhouse et al. 2003). On the contrary, earlier models focused on the mean performance of groups of individuals in discrete patches (Sutherland 1996; Rodenhouse et al. 1997; Newton 1998).

On the other hand, physical fights over breeding sites were evident during the settlement period, some birds were displaced from their territory, and older individuals were dominant over younger ones in such direct contests. Such observations are consistent with the ideal despotic model and less so with site dependence. In its original formulation (Rodenhouse et al. 1997, p. 2032, 2000, p. 1169) and subsequent theoretical treatment (McPeek et al. 2001, p. 418), the site-dependent model assumed preemptive territory occupation with no displacement, but the latter was recurrently observed in our Doñana population. Interestingly, the compatibility of site dependence with aggressive interactions is a recurrent contradictory theme in the literature. For example, Hawkins and Berryman (2000) remarked that preemption is but a form of contest competition for good-quality sites, whereas for Kokko et al. (2004), site dependence implies that one individual relegates another to a lower quality site through preemption, which still qualifies as an aggressive interaction. Finally, Rodenhouse et al. (1997, 2000, 2003) repeatedly stressed that 1) site dependence was actually derived as an extension of the despotic model, 2) it is complementary rather than alternative to it, and 3) the 2 models may simultaneously operate when density approaches saturation (i.e., under crowding conditions, Rodenhouse et al. 2003). Various lines of evidence actually suggest that the kite population of Doñana may fit such a crowding scenario. First, the population densities recorded in Doñana are the highest ever recorded for this species and extremely high in comparison with other similar-sized raptorial species (up to 10 active nests per km^2, Forero et al. 2002; Sergio et al. 2005). Second, the national park is an island of seminatural vegetation isolated within a large matrix of unfavorable intensive cultivation. Third, the population is virtually demographically closed, with extreme philopatry and virtually no immigration (Forero et al. 1999, 2002). These are the exact conditions under which crowding is most expected (Sillett et al. 2004). If the above crowding condition is true, the apparent dual support for the 2 nonexclusive models would be easily reconciled.

Therefore, our results added to a growing support for both site-dependent and despotic models of settlement (e.g., Ens et al. 1995; Petit LJ and Petit DR 1996; Zimmerman et al. 2003; Kokko et al. 2004; Rodenhouse et al. 2003; Carrete, Donázar, and Margalida 2006; review in Newton 1998). In contrast, none of the predictions of the conspecific cuing models were supported. Conspecific cuing may be more important for inexperienced individuals, which may complement direct assessments of site quality with information derived from the distribution and performance of conspecifics (e.g., Danchin et al. 2001; Sergio and Penteriani 2005). Therefore, its effect may be predictably unimportant in analyses, such as ours, which pool all individuals of a population (see Kokko et al. 2004 for similar results).

In conclusion, we believe that the evidence of site-dependent and despotic sequential settlement presented here may be generally applicable to other species for the following reasons: 1) the observed patterns fit well within the above-cited general agreement in support of the site-dependent and ideal despotic models of the distribution of breeding organisms across sites or habitats; 2) within our study species, these models gave a good fit to the observed data in 2 very distant biogeographic zones, despite enormous differences in elevation, landscape composition, climate, food availability, and population density; and 3) a review of the literature on sequential settlement uncovered a very consistent picture of state-dependent arrival, progressive monopolization of best quality sites, and cascading effects on subsequent breeding performance (Table 3). Based on the above, we propose as a general paradigm of sequential settlement for migratory species the following process, where 1) arrival date is a reliable surrogate of phenotype quality; 2) early-arriving individuals have preferential access to the best quality sites and the best quality partners; 3) the above conditions cascade into a number of benefits ultimately related to higher fitness, including higher pairing success, larger harems, earlier reproductive dates, higher chances, or rebreeding in case of failure, larger numbers of produced offspring, higher quality of the offspring, and thus higher chances of their future recruitment. Given the consistency of results across studies, despite the profound

Table 3

Review of 30 studies that investigated the association of the arrival date on territory with individual and territory quality and its consequent benefits in terms of breeding performance

	Arrival date is associated with		Early arrival implies benefits in terms of			
Species	Individual quality[a]	Territory quality	Mating success[b]	Laying date	Offspring raised	Reference
White stork *Ciconia ciconia*				1	1	Tryjanowski et al. (2004)
Black kite *Milvus migrans*[c]		1		1	1	This study[c]
Black kite[d]	1 (A, BS, BC)	1		1	1	This study[d]
Eurasian kestrel *Falco tinnunculus*	1 (A)			1		Village (1985)
Eurasian kestrel				0		Pakalongas et al. (1992)
Willow ptarmigan *Lagopus lagopus*		0		0	0	Schieck and Hannon (1992)
Pied avocet *Recurvirostra avosetta*	1 (A)				1	Hötker (2002)
Common tern *Sterna hirundo*				1		Ludwigs and Becker (2001)
Barn swallow *Hirundo rustica*	1 (A)		1 (M)		1	Møller (1990, 1994)
Cliff swallow *Petrochelidon pyrrhonota*				1		Brown CR and Brown MB (2000)
Black redstart *Phoenicurus ochruros*	1 (A)					Weggler (2000)
Black redstart	1 (A)	1				Andersson (1995)
American redstart *Setophaga ruticilla*	1 (A)		1 (M)		0	Lozano et al. (1996)
Northern wheatear *Oenanthe oenanthe*	1 (A); 0 (BC)	1	1 (M)	1	1	Currie et al. (2000)
Northern wheatear				1		Brooke (1979)
Savi's warbler *Locustella luscinioides*		1	1 (M)	1	1	Aebischer et al. (1996)
Great reed warbler *Acrocephalus arundinaceus*	1 (A)	1	1 (M, H)		1	Hasselquist (1998)[e]
Great reed warbler			1 (H)		1	Ezaki (1990)
Willow warbler *Phylloscopus trochilus*		1	1 (M, H)			Gil and Slater (2000)
Willow warbler	1 (BC); 0 (BS)			1		Arvidsson and Neergard (1991)
Dusky warbler *Phylloscopus fuscatus*	1 (BS); 0 (BC)	1				Forstmeier et al. (2001)[f]
Prothonotary warbler *Protonotoria cinerea*		1			1	Petit and Petit (1996)
Pied flycatcher *Ficedula hypoleuca*	1 (A, BS, BC)	1	1 (H)	1	1	Alatalo et al. (1984)[g]
Pied flycatcher	1 (A, BS)					Slagsvold (1986)
Pied flycatcher	1 (BS)	1	1 (M)	1	1	Potti and Montalvo (1991)
Collared Flycatcher *Ficedula albicollis*	1 (A)					Mitrus et al. (1996)
Red bishop *Euplectes orix*			1 (H)			Friedl and Klump (2000)
Great-tailed grackles *Quiscalus mexicanus*				1		Teather et al. (1988)
Red-winged blackbirds *Agelaius phoniceus*				1		Teather et al. (1988)
Red-winged blackbirds				0		Cristol and Johnsen (1994)

In each cell, 1 = relationship tested and found to be significant; 0 = relationship tested but not found to be significant; empty cell = relationship not tested by the authors.

[a] Individual quality measured as age (A), estimates of body size (BS), or indices of body condition (BC).

[b] Includes the probability of finding a mate (M) and harem size (H).

[c] Data for the Lake Lugano population (Italian Alps).

[d] Data for the Doñana population (southwestern Spain).

[e] See also Bensch and Hasselquist (1991).

[f] See also Forstmeier (2002).

[g] See also Lundberg et al. (1981) and Rätti et al. (1993).

differences in methodologies, sampled habitats, and study species (Table 3), future studies on sequential settlement should be best framed as tests of departures from such basic pattern.

Linking behavioral ecology and conservation biology

One key point in conservation biology is to find efficient ways to prioritize conservation action, so as to avoid wasting unnecessary resources on inefficient plans (e.g., Dias 1996; Sutherland 1998). Many studies have attempted to establish priorities on the basis of site quality (e.g., Poiani et al. 2001; Norris and Pain 2002; Sergio and Newton 2003; Sergio, Newton, and Marchesi 2005), but one potentially confounding factor is individual quality (Carrete, Sánchez-Zapata, et al. 2006). If site quality and individual quality are not intercorrelated, and the conservation target (e.g., offspring production) is determined by individual quality, then prioritization based on site quality alone may yield misleading results. The consistent, general pattern of phenotype-dependent, sequential settlement on progressively lower quality sites outlined in Table 3 points out arrival date as a potentially important index for prioritization exercises, capable of integrating individual and site quality, and well justified on the basis of general ecological theory (Fretwell 1972; Rodenhouse et al. 1997; Kokko 1999). Some authors have already used arrival date as a measure of habitat quality (e.g., Thomas 1984; Møller 1994; Hasselquist 1998). Our results reinforce the idea that, for migratory species, settlement date may be a reliable, integrative estimate of the combined quality of sites and of the individuals occupying them. Such consistent and integrative measures may be rare in ecology and provide a further interesting example of a potential direct link between behavioral ecology and conservation biology (Caro 1998; Gosling and Sutherland 2000).

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REFERENCES

Aebischer A, Perrin N, Krieg N, Studer J, Meyer DR. 1996. The role of territory choice, mate choice and arrival date on breeding success in the Savi's warbler. J Avian Biol. 27:143–152.

Alatalo RV, Lundberg A, Ståhlbrandt K. 1984. Female mate choice in the pied flycatcher *Ficedula hypoleuca*. Behav Ecol Sociobiol. 14: 253–261.

Andersson R. 1995. Pattern of territory establishment in males, territory quality and floaters in a marginal population of Black Redstart *Phoenicurus ochruros*. Ornis Svec. 5:143–159.

Arvidsson BL, Neergard R. 1991. Mate choice in the willow warbler—a field experiment. Behav Ecol Sociobiol. 29:225–229.

Beletsky LD, Orians GH. 1993. Factors affecting which male red-winged blackbirds acquire territories. Condor. 95:782–791.

Bensch S, Hasselquist D. 1991. Territory infidelity in the polygynous great reed warbler *Acrocephalus arundinaceus*: the effect of variation in territory attractiveness. J Anim Ecol. 60:857–871.

Berthold P. 1993. Bird migration: a general survey. Oxford: Oxford University Press.

Berthold P. 1996. Control of bird migration. London: Chapman and Hall.

Brooke ML. 1979. Differences in the quality of territories held by wheatears (*Oenanthe oenanthe*). Ibis. 48:21–32.

Brown CR, Brown MB. 2000. Nest spacing in relation to settlement time in colonial cliff swallows. Anim Behav. 59:47–55.

Burnham K, Anderson DR. 1998. Model selection and inference: a practical information theoretic approach. New York: Springer Verlag.

Caro T, editor. 1998. Behavioral ecology and conservation biology. Oxford: Oxford University Press.

Carrete M, Donázar JA, Margalida A. 2006. Density-dependent productivity depression in Pyrenean bearded vultures: implications for conservation. Ecol Appl. 16:1674–1682.

Carrete M, Sánchez-Zapata JA, Tella JL, Gil-Sánchez JM, Moleón M. 2006. Components of breeding performance in two competing species: habitat heterogeneity, individual quality and density-dependence. Oikos. 112:680–690.

Cramp S, Simmons KEL. 1980. Handbook of the birds of Europe, the Middle East and North Africa. Vol. 2: hawks and bustards. Oxford: Oxford University Press.

Crawley MJ. 1993. GLIM for ecologists. Oxford: Blackwell Science.

Cristol DA. 1995. Early arrival, initiation of nesting, and social status: an experimental study of breeding female red-winged blackbirds. Behav Ecol. 6:87–93.

Cristol DA, Johnsen TS. 1994. Spring arrival, aggression and testosterone in female red-winged blackbirds (*Agelaius phoeniceus*). Auk. 111:210–214.

Currie D, Thompson BA, Burke T. 2000. Patterns of territory settlement and consequences for breeding success in the northern wheatear *Oenanthe oenanthe*. Ibis. 142:389–398.

Danchin E, Heg D, Doligez B. 2001. Public information and breeding habitat selection. In: Clobert J, Danchin E, Dhondt AA, Nichols JD, editors. Dispersal. Oxford: Oxford University Press. p. 243–258.

Dias PC. 1996. Sources and sinks in population biology. Trends Ecol Evol. 11:326–330.

Ens BJ, Weissing FJ, Drent RH. 1995. The despotic distribution and deferred maturity: two sides of the same coin. Am Nat. 146:625–650.

Espina J. 1984. Variaciones en la alimentación de una población de milanos negros (*Milvus migrans*) [MS thesis]. [Madrid (Spain)]: University of Madrid.

Ezaki Y. 1990. Female choice and the causes of and adaptiveness of polygyny in great reed warblers. J Anim Ecol. 59:103–119.

Forero MG, Donázar JA, Blas J, Hiraldo F. 1999. Causes and consequences of territory change and breeding dispersal distance in the black kite. Ecology. 80:1298–1310.

Forero MG, Donázar JA, Hiraldo F. 2002. Causes and fitness consequences of natal dispersal in a population of black kites. Ecology. 83:858–872.

Forstmeier W. 2002. Benefits of early arrival at breeding grounds vary between males. J Anim Ecol. 71:1–9.

Forstmeier W, Kuijper DPJ, Leisler B. 2001. Polygyny in the dusky warbler, *Phylloscopus fuscatus*: the importance of female qualities. Anim Behav. 62:1097–1108.

Fransson T. 1995. Timing and speed of migration in North and West European populations of *Sylvia* warblers. J Avian Biol. 26:39–48.

Fretwell SD. 1972. Populations in a seasonal environment. Princeton (NJ): Princeton University Press.

Fretwell SD, Lucas HL. 1970. On territorial behaviour and other factors influencing distribution in birds. Acta Biotheor. 19:16–36.

Friedl TWP, Klump GM. 2000. Nest and mate choice in the red bishop (*Euplectes orix*): female settlement rules. Behav Ecol. 11:378–384.

Garnett MC. 1981. Body size, its heritability and influence on juvenile survival among great tits, *Parus major*. Ibis. 123:31–41.

Gil D, Slater PJB. 2000. Multiple song repertoire characteristics in the willow warbler (*Phylloscopus trochilus*): correlations with female choice and offspring viability. Behav Ecol Sociobiol. 47:319–326.

Gosling LM, Sutherland WJ, editors. 2000. Behaviour and conservation. Cambridge (UK): Cambridge University Press.

Gwinner E, editor. 1990. Bird migration: the physiology and ecophysiology. Berlin (Germany): Springer.

Hasselquist D. 1998. Polygyny in great reed warblers: a long-term study of factors contributing to male fitness. Ecology. 79:2376–2390.

Hawkins BA, Berryman AA. 2000. Site-dependent regulation of population size: comment. Ecology. 81:1166–1168.

Hiraldo F, Veiga JP, Mañez M. 1990. Growth of nestling black kites *Milvus migrans*: effects of hatching order, weather and season. J Zool. 222:197–214.

Hötker H. 2002. Arrival of pied avocets *Recurvirostra avosetta* at the breeding site: effect of winter quarters and consequences for reproductive success. Ardea. 90:379–387.

Kokko H. 1999. Competition for early arrival in migratory birds. J Anim Ecol. 68:940–950.

Kokko H, Harris MP, Wanless S. 2004. Competition for breeding sites and site-dependent population regulation in a highly colonial seabird, the common guillemot *Uria aalge*. J Anim Ecol. 73:367–376.

Lindström Å, Hasselquist D, Bensch S, Grahn M. 1990. Asymmetric contests over resources for survival and migration: a field experiment with bluethroats. Anim Behav. 40:453–461.

Littel RC, Milliken GA, Stroup WW, Wolfinger RS. 1996. SAS system for mixed models. Cary (NC): SAS Institute Inc.

Lõhmus A. 2003. Are certain habitats better every year? A review and case study on birds of prey. Ecography. 26:545–552.

Lozano GA, Perreault S, Lemon RE. 1996. Age, arrival date and reproductive success of male American redstarts *Setophaga ruticilla*. J Avian Biol. 27:164–170.

Ludwigs J, Becker PH. 2001. The hurdle of recruitment: influences of arrival date, colony experience and sex in the common tern *Sterna hirundo*. Ardea. 90:389–399.

Lundberg A, Alatalo RV, Carlson A, Ulfstrand S. 1981. Biometry, habitat distribution and breeding success in the pied flycatcher *Ficedula hypoleuca*. Ornis Scand. 12:68–79.

Marra PP. 2000. The role of behavioural dominance in structuring patterns of habitat occupancy in a migrant during the nonbreeding season. Behav Ecol. 11:299–308.

Marra PP, Hobson KA, Holmes RT. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. Science. 282:1884–1886.

McPeek MA, Rodenhouse NL, Holmes RT, Sherry TW. 2001. A general model of site-dependent population regulation: population-level regulation without individual-level interactions. Oikos. 94:417–424.

Mitrus C, Walankiewicz W, Czeszczewik D, Jabłoński PM. 1996. Age and arrival date of collared flycatcher *Ficedula albicollis* males do not influence quality of natural cavities used. Acta Ornithol. 31: 101–106.

Møller AP. 1990. Male tail length and female mate choice in the monogamous swallow. Anim Behav. 39:458–465.
Møller AP. 1994. Phenotype-dependent arrival time and its consequences in a migratory bird. Behav Ecol Sociobiol. 35:115–122.
Morbey YE, Ydenberg RC. 2001. Protandrous arrival timing to breeding areas: a review. Ecol Lett. 4:663–673.
Morris DW. 1988. Habitat-dependent population regulation and community structure. Evol Ecol. 2:253–269.
Morris DW. 1992. Scales and costs of habitat selection in heterogeneous landscapes. Evol Ecol. 6:412–432.
Morris DW. 1994. Habitat matching: alternatives and implications to populations and communities. Evol Ecol. 8:387–406.
Newton I, editor. 1989. Lifetime reproduction in birds. London: Academic Press.
Newton I. 1998. Population limitation in birds. London: Academic Press.
Norris K, Pain DJ, editors. 2002. Conserving bird biodiversity: general principles and their application. Cambridge (UK): Cambridge University Press.
Pakalongas P, Alatalo RV, Korpimäki E. 1992. Female choice in the kestrel under different availability of mating options. Anim Behav. 43:659–665.
Petit LJ, Petit DR. 1996. Factors governing habitat selection by prothonotary warblers: field tests of the Fretwell-Lucas models. Ecol Monogr. 66:367–387.
Poiani KA, Merrill MD, Chapman KA. 2001. Identifying conservation-priority areas in a fragmented Minnesota landscape based on the umbrella species concept and selection of large patches of natural vegetation. Conserv Biol. 15:513–522.
Potti J, Montalvo S. 1991. Male arrival and female mate choice in pied flycatchers *Ficedula hypoleuca* in Central Spain. Ornis Scand 22: 45–54.
Pöysä H. 2001. Dynamics of habitat distribution in breeding mallards: assessing the applicability of current habitat selection models. Oikos. 94:365–373.
Pulliam HR, Danielson BJ. 1991. Sources, sinks and habitat selection: a landscape perspective on population dynamics. Am Nat. 137: S50–S66.
Rätti O, Dufva R, Alatalo RV. 1993. Blood parasites and male fitness in the pied flycatcher. Oecologia. 96:410–414.
Rodenhouse NL, Sherry TW, Holmes RT. 1997. Site-dependent regulation of population size: a new synthesis. Ecology. 78: 2025–2042.
Rodenhouse NL, Sherry TW, Holmes RT. 2000. Site-dependent regulation of population size: reply. Ecology. 81:1168–1171.
Rodenhouse NL, Sillett TS, Holmes RT. 2003. Regulation of a migratory bird population by multiple density-dependence mechanisms. Proc R Soc Lond B Biol Sci. 270:2105–2110.
Schieck J, Hannon SJ. 1992. Territory and male quality do not influence settlement of yearling female willow ptarmigan. Behav Ecol. 3:148–155.
Schulte-Hostedde A, Zinner B, Millar JS, Hickling GJ. 2005. Restitution of mass-size residuals: validating body-condition indices. Ecology. 86:155–163.
Sergio F. 2003. Relationship between laying dates of black kites *Milvus migrans* and spring temperatures in Italy: rapid response to climate change? J Avian Biol. 34:144–149.
Sergio F, Blas J, Forero MG, Fernández N, Donázar JA, Hiraldo F. 2005. Preservation of wide-ranging top predators by site protection: black and red kites in Doñana National Park. Biol Conserv. 125: 11–21.
Sergio F, Newton I. 2003. Occupancy as a measure of territory quality. J Anim Ecol. 72:857–865.
Sergio F, Newton I, Marchesi L. 2005. Top predators and biodiversity. Nature. 436:192.
Sergio F, Pedrini P, Marchesi L. 2003a. Adaptive selection of foraging and nesting habitat by black kites (*Milvus migrans*) and its implications for conservation: a multi-scale approach. Biol Conserv. 112:351–362.
Sergio F, Pedrini P, Marchesi L. 2003b. Spatio-temporal shifts in gradients of habitat quality for an opportunistic avian predator. Ecography. 26:243–255.
Sergio F, Marchesi L, Pedrini P. 2003. Spatial refugia and the coexistence of a diurnal raptor with its intraguild owl predator. J Anim Ecol. 72:232–245.
Sergio F, Penteriani V. 2005. Public information and territory establishment in a loosely colonial raptor. Ecology. 86:340–346.
Sillett TS, Rodenhouse NL, Holmes RT. 2004. Experimentally reducing neighbor density affects reproduction and behavior of a migratory songbird. Ecology. 85:2467–2477.
Slagsvold T. 1986. Nest settlement by the pied flycatcher: does the female choose her mate for the quality of his house or himself? Ornis Scand. 17:210–220.
Smith JNM, Montgomerie RD, Taitt MJ, Yom-Tov Y. 1980. A winter feeding experiment on an island song sparrow population. Oecologia. 47:164–170.
Sokal RR, Rohlf FJ. 1981. Biometry. New York: W. H. Freeman.
Stamps JA. 1988. Conspecific attraction and aggregation in territorial species. Am Nat. 131:329–347.
Stephens PA, Sutherland WJ. 1999. Consequences of the Allee effect for behaviour, ecology and conservation. Trends Ecol Evol. 14:401–405.
Sutherland WJ. 1996. From individual behaviour to population ecology. Oxford: Oxford University Press.
Sutherland WJ, editor. 1998. Conservation science and action. Oxford: Blackwell Science.
Tabachnick BG, Fidell LS. 1996. Using multivariate statistics. New York: HarperCollins.
Teather KL, Muma KE, Weatherhead PJ. 1988. Estimating female settlement from nesting data. Auk. 105:196–200.
Thomas DK. 1984. Aspects of habitat selection in the sedge warbler *Acrocephalus schoenobaenus*. Bird Study. 31:187–194.
Tryjanowski P, Sparks TH, Ptaszyk J, Kosicki J. 2004. Do white storks *Ciconia ciconia* always profit from an early return to their breeding grounds? Bird Study. 51:222–227.
Village A. 1985. Spring arrival times and assortative mating of kestrels in South Scotland. J Anim Ecol. 54:857–868.
Viñuela J. 1993. Variacion en la fecha de puesta de una poblacion de Milano Negro (*Milvus migrans*). Efecto de la experiencia de los reproductores. Ardeola. 40:55–63.
Viñuela J, Bustamante J. 1992. Effect of growth and hatching asynchrony on the fledging age of black kites and red kites. Auk. 109:748–757.
Weatherhead PJ, Robertson RJ. 1979. Offspring quality and the polygyny threshold: "the sexy son hypothesis." Am Nat. 113: 201–208.
Weggler M. 2000. Reproductive consequences of autumnal singing in black redstarts (*Phoenicurus ochruros*). Auk. 117:65–73.
Wiley RH. 1981. Social structure and individual ontogenies: problems of description, mechanism and evolution. In: Bateson PPG, Klopfer PH, editors. Perspectives in ethology. New York: Plenum. p. 261–293.
Zimmerman GS, LaHaye WS, Gutierrez RJ. 2003. Empirical support for a despotic distribution in a California spotted owl population. Behav Ecol. 14:433–437.